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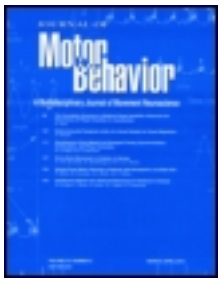

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C. (Lieke) E. Peper [a], Suzanne A. E. Nooij [a] & A. J. (Knoek) van Soest [a]
[a] Institute for Fundamental and Clinical Human Movement Sciences Amsterdam/Nijmegen [b] Vrije Universiteit Faculty of Human Movement Sciences Amsterdam, The Netherlands

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Mass Perturbation of a Body Segment: 2. Effects on Interlimb Coordination

C. (Lieke) E. Peper
Suzanne A. E. Nooij
A. J. (Knoek) van Soest
Institute for Fundamental and Clinical Human Movement Sciences, Amsterdam/Nijmegen, and
Faculty of Human Movement Sciences
Vrije Universiteit, Amsterdam, The Netherlands

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ABSTRACT. The shifts in relative phase that are observed when rhythmically coordinated limbs are submitted to asymmetric mass perturbations have typically been attributed to the induced eigenfrequency difference ($\Delta\omega$) between the limbs. Modeling the moving limbs as forced linear oscillators, however, reveals that asymmetric mass perturbations may induce a difference not only in eigenfrequency (i.e., $\Delta\omega \neq 0$) but also in the covarying low-frequency control gains (i.e., $\Delta k \neq 0$). Because the inverse of the low-frequency control gain (k) reflects the level of muscular torque (input) required for a particular displacement from equilibrium (output), asymmetric mass perturbations may result in an imbalance in the muscular torques required for task performance (related to $\Delta k \neq 0$). Thus, it is possible that the effects attributed to $\Delta\omega$ were in fact mediated by Δk. In 2 experiments, the authors manipulated Δk and $\Delta\omega$ separately by applying mass perturbations to the lower legs of 9 participants. The relative phasing between the legs was not affected by Δk, but manipulation of $\Delta\omega$ (while Δk remained approximately 0) induced systematic relative phase shifts that were more pronounced for antiphase than for in-phase coordination. That indication that the coordination dynamics is indeed influenced by an imbalance in eigenfrequency is discussed vis-à-vis the question of how such a merely peripheral property may affect the underlying coordination process.

Key words: eigenfrequency, interlimb coordination, low-frequency control gain, mass perturbation, relative phase

Rhythmic interlimb coordination is characterized by interactions between the limbs. Because of those interactions, only a limited number of coordination patterns can be adequately performed without specific training. For instance, when two identical limbs are moved at the same frequency, the coordination between them is attracted to one of two stable coordination patterns (e.g., Tuller & Kelso, 1989; Yamanishi, Kawato, & Suzuki, 1980): in-phase (phase difference between the limbs or *relative phase* $\varphi = 0$) or antiphase ($\varphi = \pi$). Those coordination tendencies are affected by peripheral aspects of the limbs involved. A well-documented example of that influence is observed when limbs with different inertial properties (e.g., an arm and a leg) are coordinated or when one creates an asymmetry between the limbs by means of mass addition or by using combinations of hand-held, physical pendulums that differ in mass distribution. In such cases, attraction to stable coordination patterns may still occur, but the resulting phase relations are slightly shifted with regard to the symmetric situation (e.g., Rosenblum & Turvey, 1988; Schmidt, Shaw, & Turvey, 1993; Sternad, Collins, & Turvey, 1995; Sternad, Turvey, & Schmidt, 1992). Those shifts in relative phase, which reflect a coordinative asymmetry in which one of the limbs is slightly leading in time, are more pronounced for (intended) antiphase coordination than for (intended) in-phase coordination. In fact, depending on the tempo of performance and the degree of dissimilarity between the limbs induced by mass addition (or variations in the mass distribution of hand-held, physical pendulums), a variety of behaviors may be observed, including shifts in relative phase and reduced coordinative stability (cf., Schmidt & Turvey, 1995), phase wrapping (e.g., Kelso & Jeka, 1992), and preferential routes in frequency-induced transitions (Jeka & Kelso, 1995).

Most interesting, those phenomena can all be explained on the basis of a simple extension of the well-known Haken-Kelso-Bunz (HKB) potential for rhythmic interlimb coordination (Haken, Kelso, & Bunz, 1985), in which the coordinative symmetry (i.e., $-\varphi = \varphi$) is broken by means of an additional detuning term (Kelso, DelColle, & Schöner, 1990):

$$V(\varphi) = -\delta \cdot \phi - a \cdot \cos \phi - b \cdot \cos 2\phi, \quad (1)$$

Correspondence address: C. E. Peper, Faculty of Human Movement Sciences, Vrije Universiteit, Van der Boechorststraat 9, 1081 BT Amsterdam, The Netherlands. E-mail address: C_E_Peper @FBW.VU.NL

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where the two cosine terms constitute the original HKB potential (Haken et al., 1985), whereas the first term reflects the effect of detuning. The potential captures the changes in the relative phase dynamics that are observed when one creates an asymmetry between the oscillating components by means of manipulations that affect their moments of inertia, be it by adding mass to a segment (e.g., Jeka & Kelso, 1995) or by using hand-held, physical pendulums that differ in mass distribution (e.g., E. L. Amazeen, Sternad, & Turvey, 1996; Sternad, Amazeen, & Turvey, 1996). In this article, such manipulations are referred to as *mass perturbations*. Because δ is simply a parameter that induces an asymmetry in the potential, Equation 1 is indifferent to the way in which that parameter is related to the experimental manipulations. On the basis of a large body of empirical evidence, however, δ (and, thus, the origin of the observed changes in interlimb coordination) has been inferred to correspond to the difference in eigenfrequency (commonly referred to as $\Delta\omega$) between the oscillating components (e.g., E. L. Amazeen et al., 1996; Jeka & Kelso, 1995; Kelso et al., 1990; Kelso & Jeka, 1992). Indeed, systematic manipulations of the (undamped) eigenfrequencies[1] of hand-held pendulums revealed that the deviation of relative phase from the intended coordination pattern (in-phase or antiphase), denoted by $\Delta\varphi$, increased with $\Delta\omega$ and was accompanied by a decrease in coordinative stability (cf. Schmidt & Turvey, 1995).

Equation 1 does not, however, explain why differences in eigenfrequency result in the corresponding relative phase dynamics. To elucidate that relation, one needs a model that allows for linking the extended HKB potential (i.e., Equation 1) to the segment property of interest (i.e., eigenfrequency). A logical entry point in that regard is formed by the system of nonlinearly coupled oscillators that was proposed by Haken et al. (1985) to reveal how the stability features of the original (symmetric) HKB potential may result from the spatiotemporal characteristics of the limb movements and their interactions. Extending that model of coupled oscillators to a situation in which the eigenfrequencies are modulated by means of mass perturbations may seem trivial at first sight: By adjusting the stiffness parameters (defined in terms of unit mass) in the limit cycle oscillators, one can alter their oscillation frequencies (i.e., eigenfrequencies; cf. Daffertshofer, Van den Berg, & Beek, 1999; Fuchs, Jirsa, Haken, & Kelso, 1996). The actual movement frequency is not solely dependent on the limb's mechanical eigenfrequency, however, because, evidently, we can force our limbs to move at various frequencies. In this context, it is useful to note that the proposed limit cycle oscillators are autonomous (i.e., undriven) oscillators that capture the kinematic characteristics of the movements of the individual limbs, without dissociating between influences of particular, for example, neurophysiological or biomechanical, properties of the movement system (see, e.g., Beek, Rikkert, & Van Wieringen, 1996; Kay, Kelso, Saltzman, & Schöner, 1987). When the movements of a single limb are modeled in that way, accommodation of voluntary frequency adjustments also entails stiffness modulations that, technically, modify the oscillator's eigenfrequency. Thus, according to this perspective, all changes in the frequency of oscillation of an (uncoupled) rhythmically moving limb are to be accounted for in terms of modulations of the oscillator's stiffness parameter. Therefore, the model does not readily allow for dissociating between parameter modulations associated with voluntary selection of a required or intended movement frequency and those associated with mechanical manipulations that alter the limb's eigenfrequency (e.g., by means of mass perturbation).

A more expedient means to address the way in which mass perturbations inflict changes in the coordination dynamics is provided by models that dissociate between peripheral aspects of the effector system and the neural control over those effectors, such as the model construct suggested by Beek, Peper, and Daffertshofer (2002; see also Peper & Beek, 1998; Peper, Beek, & Daffertshofer, 2000) in which each individual limb is modeled as a system of two bidirectionally coupled oscillators (for related model constructs, see e.g., Fuchs, Jirsa, & Kelso, 2000; Hatsopoulos, 1996; Jirsa, Fuchs, & Kelso, 1998; Jirsa & Haken, 1997; Sternad, Saltzman, & Turvey, 1998). Beek et al. (2002) proposed modeling the end-effectors (the limbs) by means of linearly damped oscillators, whereas the neural oscillators are considered to be self-sustaining (i.e., limit cycle) oscillators. Each neural oscillator forces the associated effector oscillator and is, in turn, affected by the latter because of movement-related afferences. This two-level structure not only reproduces the stability characteristics of rhythmic single-limb movements but also allows for an adequate account of various aspects of such movements that are not captured by single limit cycle oscillators (see Beek et al., 2002, for details). At the same time, the archetypal dynamics of rhythmic interlimb coordination (as captured by the HKB potential) are preserved when the neural oscillators associated with two individual limb segments are nonlinearly coupled (Beek et al., 2002). Moreover, the proposed structure provides new tools for addressing the way in which the identified coordination dynamics result from particular system properties and interaction processes (cf. Peper, Daffertshofer, & Beek, 2004). As such, this model offers an adequate perspective for addressing the way in which (bio)mechanical eigenfrequency differences affect the interlimb coordination dynamics.

Effects of Mass Perturbations on Effector Dynamics

According to the just-mentioned two-level model construct (or related models involving a forced linearly damped effector oscillator, e.g., Hatsopoulos, 1996; Jirsa & Haken, 1997; Sternad et al., 1998), adding mass to a limb segment modifies the corresponding effector oscillator (and might, because of resulting changes in the afferent signals, also affect the associated neural oscillator and neural coupling). Thus, the effects of asymmetric mass perturbations on the

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interlimb coordination dynamics are mediated by the induced modifications of the dynamics of the effector oscillator. In the current study, we aimed to identify which characteristics of the effector dynamics play an essential role in that regard. To that end, we took our starting point in the results of Van Soest, Peper, & Selles (2004), who examined how mass perturbations affect essential properties of a limb segment that was modeled as a linearized driven physical pendulum (i.e., a pendulum with distributed mass) with additional joint stiffness, defined by

$$I \cdot \ddot{\varphi} + B \cdot \dot{\varphi} + (K_g + K) \cdot \varphi = T,$$

with

$$I = \sum m_i \cdot R_{gyr,i}^2 = m \cdot R_{gyr}^2 + \Delta m \cdot R^2$$

and

$$K_g = g \cdot \sum m_i \cdot R_i = g \cdot (m \cdot R_{cm} + \Delta m \cdot R), \quad (2)$$

where φ is segment displacement from equilibrium, m_i is the mass of a given component, $R_{gyr,i}$ is its radius of gyration relative to the pivot point, R_i is the distance between its center of mass and the pivot point, m is (unperturbed) segment mass, R_{gyr} is the radius of gyration of the (unperturbed) limb segment relative to the pivot point, R_{cm} is the distance between the pivot point and the (unperturbed) segment's center of mass, Δm is the added mass, R is its distance to the pivot point, g is the acceleration caused by gravity, I is the segment's moment of inertia, B is joint rotational damping, K_g is gravitational stiffness, K is joint rotational stiffness, and T is the applied muscular torque. (For details, see Van Soest et al., 2004. Note that for our current purposes, we have simplified the notation slightly, using B, K, and T rather than B_{Tp}, K_{Tp}, and T_{act}, as was used by Van Soest et al.; furthermore, we confine the current presentation to oscillations centered around $\varphi = 0$. For related modeling involving a linear forced oscillator, see, e.g., Fuchs et al., 2000; Hatsopoulos, 1996; Jirsa et al., 1998; Jirsa & Haken, 1997.) To characterize that system in terms of standard parameters, Van Soest et al. (2004) related it to the following standard form for the equation of motion of a linear second-order differential equation (cf., e.g., Doebelin, 1998):

$$\frac{1}{\omega_0^2} \cdot \ddot{\varphi} + 2 \cdot \frac{\beta}{\omega_0} \cdot \dot{\varphi} + \varphi = k \cdot T, \quad (3)$$

where ω_0 is the system's undamped eigenfrequency, β is the relative damping, and k is the low-frequency control gain. (For details see Van Soest et al. Note that we have simplified the notation by using k rather than k_{act}, as used by Van Soest et al.; in addition, note that k represents low-frequency control gain, whereas K represents joint rotational stiffness). Thus, one can determine the influence of mass addition on the system properties ω_0, β, and k by relating Equation 2 to Equation 3.

The results revealed how the effector oscillator's eigenfrequency is affected by mass perturbations (depending on both the mass itself and its distance from the pivot point; for more details, see the following). However, the effects of mass addition onto the effector's dynamics are not confined to changes in its eigenfrequency. Most interesting, as is outlined next, mass perturbations also affect the segment's low-frequency control gain (Van Soest et al., 2004). That observation implies that eigenfrequency manipulations (by means of mass addition or by variations in the mass distribution of hand-held, physical pendulums) are always associated with changes in the corresponding low-frequency control gain. Therefore, in spite of the large number of studies in which manipulations of $\Delta\omega$ were shown to result in coordinative asymmetries, the interpretation that those asymmetries were indeed caused by the created imbalance in eigenfrequency may still be questioned on the basis of the proposed model of the effector dynamics, because the effects of the imposed difference in eigenfrequency were not dissociated from the effects of the covarying difference in the segments' low-frequency control gains.

The term *low-frequency control gain* (k, also referred to as *steady-state gain* or *static sensitivity*; cf. Doebelin, 1998) stems from linear systems theory. One can directly deduce its interpretation by considering the steady-state solution of Equation 3 (i.e., $\ddot{\varphi} = 0$, $\dot{\varphi} = 0$) in case of a constant input, resulting in $\varphi_{steady\text{-}state} = k \cdot T_{steady\text{-}state}$. In other words, a particular torque $T_{steady\text{-}state}$ results in a steady-state value of φ equaling $k \cdot T_{steady\text{-}state}$. Put differently, the constant torque required for a particular constant displacement from equilibrium equals $1/k$. In terms of sinusoidal movements (resulting from sinusoidal forcing), k is directly related to the ratio of the amplitude of $\varphi(t)$ over the amplitude of $T(t)$, with, for very low frequencies (i.e., in the limit $\omega \to 0$), k exactly equaling that ratio (hence, the term *low-frequency* control gain). In relation to the present study, the most relevant feature to consider is that, at any frequency of oscillation, a relative change in k results in an identical relative change in that ratio (e.g., see Doebelin, 1998). Thus, for any frequency of oscillation, a decrease in k implies a proportional increase in the joint torque that is required to produce a particular movement amplitude.

As was demonstrated in the accompanying study by Van Soest et al. (2004), the low-frequency control gain is reduced by mass addition. For the linear system presented earlier, that relation is defined by

$$k = \frac{1}{K_g + K},$$

with

$$K_g = g \cdot \sum m_i \cdot R_i = g \cdot (m \cdot R_{cm} + \Delta m \cdot R) \quad (4)$$

as can be readily appreciated by relating Equation 2 to Equation 3. Equation 4 reveals that k is in fact the inverse of the effective stiffness (resulting from both joint stiffness K and gravitational stiffness K_g) and is thus dependent on both the added mass (Δm) and its distance to the rotation point (R). Mass addition results in a decrease in k (for $R > 0$; cf. Equation 4), which implies that a larger muscular torque is

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required to generate a particular amplitude of oscillation. Clearly, applying different mass perturbations to two homologous limbs may invoke an asymmetry in low-frequency control gain (i.e., $\Delta k \neq 0$) and, consequently, in the net joint torques required for similar performance. As such, it is possible that the effects that have been attributed to a difference in eigenfrequency were in fact mediated by the covarying difference in low-frequency control gain and thus induced by an imbalance in the required muscular torque.

In that context, it is useful to reconsider the empirical findings of Jeka and Kelso (1995), which were originally interpreted in terms of the effects of asymmetries in eigenfrequency. Referring to several experiments with hand-held pendulums (e.g., Kugler & Turvey, 1987; Rosenblum & Turvey, 1988; Sternad et al., 1992), Jeka and Kelso chose to manipulate the eigenfrequency difference by changing the inertial properties of the limb segments. In their experiment, adding mass to the lower arm decreased the difference in the inertial properties between the lower arm and the lower leg, whereas adding mass to the lower leg increased the difference in those properties. In agreement with their predictions, the phase shift ($\Delta\varphi$) increased when the leg was loaded, whereas it decreased when the arm was loaded. Thus, those results suggested that the coordinative asymmetries were indeed caused by the eigenfrequency difference between the limbs.

However, inducing the desired modification of a segment's eigenfrequency by means of mass perturbation requires careful positioning of the mass in relation to the segment's anthropometry (cf. Van Soest et al., 2004). Whereas the eigenfrequency of an ideal, point-mass pendulum depends simply on the length of the pendulum (representing the distance between the pivot point and the point mass), for a physical pendulum (i.e., a pendulum with a particular mass distribution and, in our case, an additional stiffness parameter), the situation is more complicated. Relating Equation 2 to Equation 3 reveals that the undamped eigenfrequency of the proposed linear system is defined by

$$\omega_0 = \sqrt{\frac{K_g + K}{I}},$$

with

$$I = \sum m_i \cdot R_{gyr,i}^2 = m \cdot R_{gyr}^2 + \Delta m \cdot R^2,$$

and

$$K_g = g \cdot \sum m_i \cdot R_i = g \cdot (m \cdot R_{cm} + \Delta m \cdot R) \quad (5)$$

(cf. Van Soest et al., 2004). Because adding mass influences both the numerator and the denominator of the ratio in Equation 5 (which represent the system's effective stiffness and inertia, respectively), it is not instantly clear what the effect on the resulting undamped eigenfrequency (ω_0) will be. In particular, the fact that the contribution of the effective stiffness is linearly related to the distance (R) between the pivot point and the added mass, whereas the contribution of effective inertia is related to R^2, results in an interesting nonmonotonical relation between R and ω_0.

To gain more insight in that regard, Van Soest et al. (2004) introduced parameter R_0 as being the length of a point-mass pendulum with an undamped eigenfrequency identical to that of the (unperturbed) limb segment:

$$R_0 = \frac{R_{gyr}^2}{R_{cm} + \frac{K}{m \cdot g}}. \quad (6)$$

If we consider Equation 6 for the hypothetical situation $K = 0$, it is directly clear that for our physical pendulum, $R_0 > R_{cm}$ (because $R_{gyr} > R_{cm}$), whereas for a point-mass pendulum, per definition, $R_0 = R_{cm}$. Using Equation 6, one can express the influence of particular locations of mass addition onto the undamped eigenfrequency of a limb segment (with $K \geq 0$) in relation to R_0: Evidently, given the definition of R_0, mass added at $R = R_0$ leaves ω_0 unaffected; mass applications at distances $0 < R < R_0$ yield a nonmonotonical increase in ω_0; for mass addition at $R > R_0$, ω_0 decreases (see Figure 1A).[2] Note that the observed nonmonotonical relation between R and ω_0 is essentially different from that obtained for a point-mass pendulum, for which ω_0 decreases monotonically with increasing pendulum length (i.e., with increasing distance between the pivot point and the point mass).

For the lower leg + foot segment, R_0 is located close to the ankle joint (cf. Plagenhoef, Evans, & Abdelnour, 1983), which was in fact the location of mass addition in the study of Jeka and Kelso (1995).[3] Thus according to the results of Van Soest et al. (2004), the applied mass perturbation hardly affected the undamped eigenfrequency of that limb segment and, consequently, the empirical findings of Jeka and Kelso may not have been caused by variations in $\Delta\omega$. Given the decrease in low-frequency control gain that occurs when mass is added to a limb segment (cf. Equation 4; see also Figure 1B), it is possible that the observed changes in coordination were instead induced by the invoked changes in low-frequency control gain.

Aim in the Present Study

The analysis of the effects of mass perturbations on the effector dynamics (with the limb segment being modeled as a forced second-order system) revealed that in previous experiments in which the effects of asymmetries in eigenfrequency on the interlimb coordination dynamics were examined, the covarying differences in low-frequency control gain were a potentially confounding factor. Therefore, we conducted the present study to determine whether the coordination phenomena that have typically been attributed to a difference in eigenfrequency ($\Delta\omega$) may in fact be the result of a difference in the covarying low-frequency control gain (Δk). To that end, we dissociated the effects of the undamped eigenfrequencies and low-frequency control gains of the limb segments (or, in

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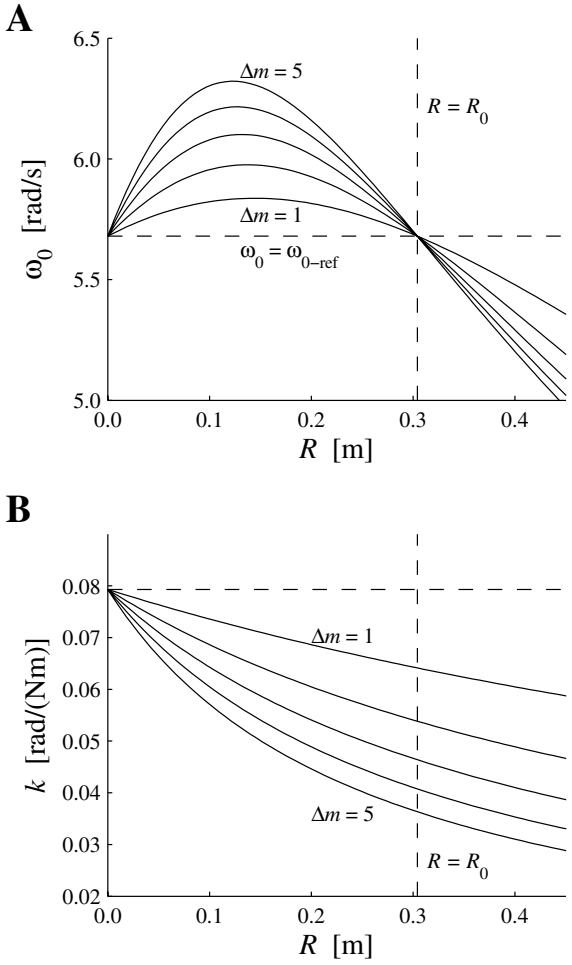

FIGURE 1. Undamped eigenfrequency (ω_0; **Panel A**) and low-frequency control gain (k; **Panel B**) of a physical pendulum as a function of mass perturbation, determined on the basis of Equations 5 and 4, respectively for a male participant's lower leg + foot segment (segment length = 0.41 m, m = 4.2 kg, K = 2.19 Nm·rad^{-1}, R_{cm} = 0.250 m, and R_{gyr} = 0.303 m, resulting in R_0 = 0.304 m). The separate curves were obtained for five different added masses (Δm = 1, 2, 3, 4 and 5 kg; the masses associated with the outermost curves are indicated in the graphs). R = distance between added mass and pivot point; R_0 = length of corresponding point mass pendulum (cf. Equation 6); R_{gyr} = radius of gyration of the (unperturbed) limb segment relative to the pivot point; R_{cm} = distance between the pivot point and the (unperturbed) segment's center of mass; $\omega_{0\text{-ref}}$ and k_{ref} reflect the values obtained in the absence of mass perturbation. Adapted from Van Soest et al. (2004).

model terms, effector oscillators) on interlimb phasing in two experiments. We applied mass perturbations to the lower legs to manipulate the uncoupled eigenfrequencies, the low-frequency control gains, or both, of those limb segments. In the first experiment, the mass perturbations were applied in such a way that the undamped eigenfrequencies of the two legs were similar ($\Delta\omega \approx 0$), whereas the difference in low-frequency control gain varied ($\Delta k \neq 0$). If coordinative asymmetries are determined by $\Delta\omega$, then no phase shifts or changes in coordinative stability were to be expected. If, however, an imbalance in low-frequency control gain results in coordinative asymmetries, then increasing values of Δk should result in increasing deviations from the intended coordination patterns together with decreasing stability of performance. The second experiment adhered to the same logic, but the manipulations were reversed: Mass perturbations were chosen that induced variation in $\Delta\omega$ ($\Delta\omega \neq 0$), while resulting in similar values of k ($\Delta k \approx 0$).

EXPERIMENTS 1 and 2

We designed two experiments to examine the effects of $\Delta\omega$ and Δk (as defined for the corresponding effector oscillators) on the relative phasing between the lower legs. We achieved manipulation of those two variables by differential loading of the limb segments in question. As can be seen in Figure 1, adding weight to a lower leg has different effects on ω_0 and k: Whereas ω_0 can either be increased (by attaching a weight relatively close to the knee) or decreased (by attaching a weight at a larger distance from the knee), k decreases in both cases. By loading the left and right legs with different weights at different distances from the knee, one can separately manipulate $\Delta\omega$ and Δk, as is illustrated in the following. Because the influence of damping on the frequency of oscillation of a limb segment is negligibly small (cf. Van Soest et al., 2004), we used the undamped eigenfrequency ω_0 as an estimate of the damped eigenfrequency of the limb segment (effector oscillator).

For each participant, we used the following equations (cf. Equations 5 and 4) to estimate the effect of loading on ω_0 and k of the effector oscillators:

$$\omega_0 = \sqrt{\frac{K_g + K}{I_{leg} + I_{lever} + I_{disc}}}, \tag{7}$$

$$k = \frac{1}{K_g + K}, \tag{8}$$

with, for both Equations 7 and 8,

$$K_g = g \cdot \sum m_i \cdot R_i = g \cdot (m_{leg} \cdot R_{leg} + m_{lever} \cdot R_{lever} + m_{disc} \cdot R_{disc}),$$

where m represents the mass of each component (i.e., leg, lever, or disc), R represents the distance between the center of mass of each component and the pivot point, I is the moment of inertia of those components relative to the pivot point ($I = m \cdot R_{gyr}^2$), g is the acceleration caused by gravity, K_g is gravitational stiffness, and K represents joint rotational stiffness. The characteristics of the lower leg + foot segment were estimated, following Plagenhoef et al. (1983), on the basis of gender, body weight, and segment length of the lower leg and foot. In addition, the characteristics of the

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experimental set-up, involving a lever and an ankle support (in Equations 7 and 8, together denoted by *lever*), were taken into account.

In Figure 2, we illustrate how, on the basis of Equations 7 and 8, we chose load combinations that satisfied the requirements of the two experiments. One can meet the requirements of Experiment 1 ($\Delta\omega \approx 0$, $\Delta k \neq 0$) by exploiting the nonmonotonical relation between R and ω_0; for example, by attaching to the left leg a weight of 5 kg at distance $R_{\text{disc-left}} = R_0$ while keeping the right leg unloaded (Figure 2A). That load combination results in similar undamped eigenfrequencies but different low-frequency control gains for the two legs. One accomplishes the opposite situation (Experiment 2: $\Delta\omega \neq 0$, $\Delta k \approx 0$) by, for example, attaching to the right leg a weight of 5 kg relatively close to the knee (at $R_{\text{disc-right}}$) and attaching to the left leg a weight of 2 kg at a larger distance from the knee (at $R_{\text{disc-left}}$; see Figure 2B). In that way, it is possible to make sure that the low-frequency control gain of the right leg is similar to that of the left leg (i.e., $k_{\text{right}} \approx k_{\text{left}}$), while the undamped eigenfrequency of the right leg differs from that of the left leg ($\omega_{0\text{-right}} \neq \omega_{0\text{-left}}$). Note that for this experiment, it was necessary to apply mass perturbations to both limb segments: Although one may induce a difference in eigenfrequency by simply adding mass to one of the segments, that manipulation also affects the low-frequency control gain of that segment. That implies that to create similar low-frequency control gains for the two segments involved, one also has to load the other segment. Thus, the requirements of Experiment 2 can be met only by applying particular combinations of mass and mass distance to the two limb segments.

The stiffness term K in Equations 7 and 8 represents joint rotational stiffness. When the muscular contribution is low, joint stiffness may be assumed to be negligible. However, pilot measurements revealed that the empirically obtained eigenfrequency of the leg–lever system that was used in the experiments (see Method section) tended to exceed the eigenfrequency estimated on the basis of Equation 7 with $K = 0$. Although such an increased stiffness level is in line with the results of several previous studies (e.g., Bingham, Schmidt, Turvey, & Rosenblum, 1991; Hatsopoulos & Warren, 1996), in the current situation the estimated K values were found to be largely influenced by the experimental set-up: Comparison of the preferred frequencies obtained when the participants oscillated their lower legs freely (pilot measurements for which we used an Optotrak system, Northern Digital, Inc., Waterloo, Ontario, for movement registration) with those obtained for oscillations produced in the experimental set-up indicated that the difference in eigenfrequency was caused mainly by the fact that the momentary axis of rotation of the knee shifted during movement. As a result, the oscillatory movements of the lower leg involved a varying displacement of the joint's (shifting) axis of rotation relative to the fixed rotation axis of the lever to which the lower leg was attached, resulting in an additional restoring force. To correct for the observed difference in eigenfrequency, we estimated the rotational stiffness parameter K for the leg–lever system for each participant before the experiments.

Thus, the mass perturbations that were required to create the desired experimental conditions were based on estimations regarding anthropometry and the rotational stiffness of

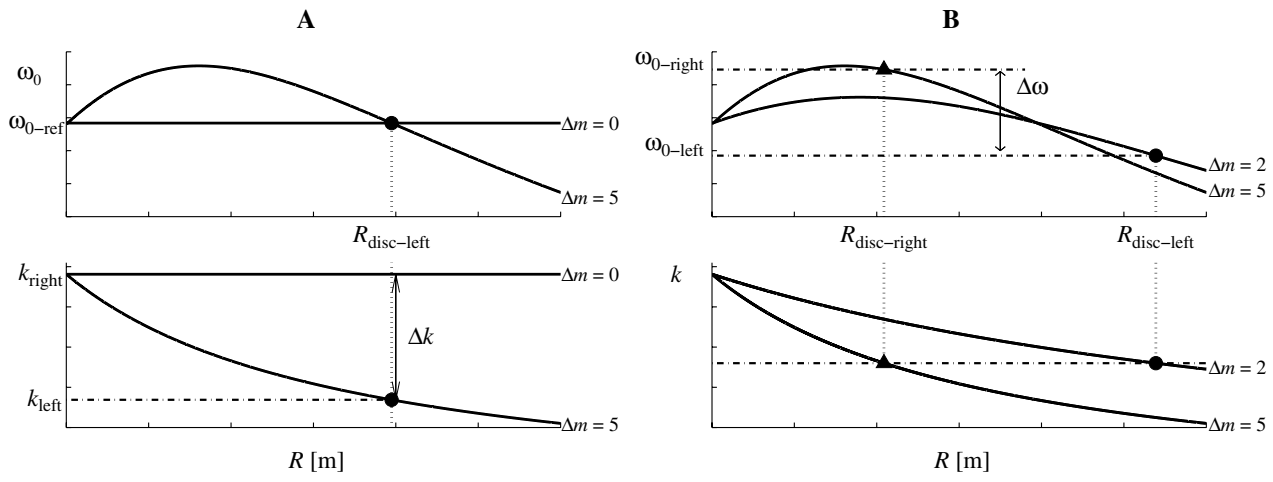

FIGURE 2. Illustration of the way in which mass perturbations were selected that met the requirements of Experiments 1 and 2. Equations 5 and 4 formed the basis for generating the graphs for ω_0 and k, respectively. R = distance between added mass and pivot point, Δm = added mass, $\omega_{0\text{-ref}} = \omega_0$ in the absence of mass perturbation. (**Panel A**) Experiment 1 ($\omega_{0\text{-right}} = \omega_{0\text{-left}} = \omega_{0\text{-ref}}$, $k_{\text{right}} \neq k_{\text{left}}$): Right leg is unloaded, left leg is loaded with 5 kg attached at distance $R_{\text{disc-left}} = R_0$ (i.e., the distance at which $\omega_{0\text{-left}} = \omega_{0\text{-ref}}$ and, thus, $\omega_{0\text{-left}} = \omega_{0\text{-right}}$; upper graph). That manipulation affects k_{left}, whereas k_{right} remains unaffected (lower graph). (**Panel B**) Experiment 2 ($\omega_{0\text{-right}} \neq \omega_{0\text{-left}}$, $k_{\text{right}} = k_{\text{left}}$): Right leg (triangles) is loaded with 5 kg attached at $R_{\text{disc-right}}$, left leg (circles) is loaded with 2 kg attached at $R_{\text{disc-left}}$. The use of two different masses allows one to select $R_{\text{disc-right}}$ and $R_{\text{disc-left}}$ in such a way that $k_{\text{right}} = k_{\text{left}}$ (lower graph), whereas $\omega_{0\text{-right}} \neq \omega_{0\text{-left}}$ (upper graph).

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the leg–lever system, which were determined for each participant individually. Because estimation errors may have caused small errors in the induced values of ω_0 and k, it is useful to consider the potential impact of such errors on the interpretation of the experimental results. First, we estimated the characteristics of the lower leg + foot segment by using averaged anthropometric features, as determined by Plagenhoef et al. (1983) for healthy males in the same age group as the (male) participants in the current experiments. Although individual variations in the actual mass distribution of the lower leg + foot segment may have resulted in small errors in the estimated values of ω_0 and k, those variations were anticipated to be distributed randomly over participants, implying that no systematic influences of those estimation errors were to be expected.

Second, the estimations were based on the assumption that K remained invariant over the experimental conditions. Indications that joint stiffness may vary as a function of inertial loading (Baldissera & Cavallari, 2001; but see also Ridderikhoff, Peper, Carson, & Beek, 2003) suggest that given that assumption, systematic variations in the induced values of ω_0 and k may have occurred. However, in the current context, the influence of such active modulations of joint stiffness on those variables is negligibly small compared with the contributions of the gravitational stiffness K_g (i.e., $g \cdot [m_{leg} \cdot R_{leg} + m_{lever} \cdot R_{lever} + m_{disc} \cdot R_{disc}]$ in Equations 7 and 8) and the rotational stiffness associated with the experimental set-up (which partly determined K in Equations 7 and 8). Nevertheless, to minimize any potential impact of variations in joint stiffness, we based the experimental manipulations on a K value that was estimated for an intermediate level of loading (see Method section). In addition, note that small increases in K as a function of loading would typically lead to amplification of the created asymmetries in the $\Delta\omega \neq 0$ and $\Delta k \neq 0$ conditions, thereby warranting adequate examination of our research question.

The required effort (i.e., muscular torque) is affected not only by the low-frequency control gain (k) but also by the amplitude of the movements. To evaluate the way in which an imbalance in low-frequency control gain affects the relative phasing and stability of rhythmic interlimb coordination, we instructed participants to maintain a steady, prescribed amplitude over the course of the experiment. Because the calculations were based on linear approximations assuming small oscillation amplitudes (cf. Van Soest et al., 2004), the prescribed amplitude was relatively small (14°, i.e., movement range of 28°). That small amplitude also ensured that the oscillations were centered approximately around the vertical (cf. Van Soest et al.).

Method

Participants

Nine (19- to 30-year-old) male undergraduate and postgraduate students at the Vrije Universiteit Amsterdam participated in this study. For all participants, body weight and length of the lower legs (i.e., the distance between the epicondylus femoris lateralis and the center of the malleolus lateralis) were measured (cf. Table 1). Because the lengths of the right and left legs were similar, averaged leg length was used in Equations 7 and 8.

Experimental Set-up

Participants sat in a chair, designed especially for these experiments, that allowed free swinging of the lower leg + foot segment. The chair consisted of a metal frame with a wooden seat and backrest that were adjustable to the measures of each individual participant. The lower legs were secured to an aluminum lever (length = 0.7 m, mass = 0.56 kg; with an additional ankle support, mass = 0.80 kg) attached to the chair frame, which allowed rotation in the sagittal plane. The joint angle was registered by a potentiometer (Sakae [Kawasaki-city, Japan], Type FCP40A-5k, sensitivity < 0.1°) mounted on the lever and connected to a computer. Sampling frequency was 400 Hz. For each individual participant, the position of the axis of rotation was aligned with the knee joint. Metal discs (mass = 1–5 kg, diameter = 0.07–0.15 m) could be secured to the outside of the lever to alter the mechanical characteristics of the leg–lever system. In Experiment 1, the participants wore a headphone through which a computer-generated pacing signal was presented.

Procedure

The measurements involved four parts: a pretest in which we estimated stiffness parameter K, Experiment 1 (manipulation of Δk), Experiment 2 (manipulation of $\Delta\omega$), and a posttest in which we investigated whether the parameter estimations for K remained constant during the experiment. The tests were carried out in two separate sessions. The first session involved the pretest only (approximately 0.45 hr); the second session involved the other three parts (approximately 4.0 hr). The period between the sessions varied from 1 hr to 1 day. We presented short breaks between the parts of the second session to minimize fatigue.

The participants sat in the chair; their lower legs were attached to the levers. Participants wore sports pants and had removed their shoes. They were instructed to move either one or both lower legs rhythmically at a constant frequency and amplitude, using minimal effort. The experimenter monitored movement amplitude (A) on an oscilloscope, which enabled her to instruct the participant to adjust the amplitude until the desired amplitude was reached ($A = 14° \pm 3°$; note that movement range = $2A$ = 28°). That amplitude was to be maintained during the rest of the trial. When performance had been stabilized at the desired amplitude, the experimenter started data collection and recorded the knee angle during 25 s. After each trial, mean movement amplitude and frequency as attained in that trial were automatically calculated. If the averaged amplitude was outside the desired range, the trial was rerun. That occurred 3–6 times per participant, predominantly in Experiment 2.

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TABLE 1. Anthropometric Characteristics and Resulting Manipulations for Experiment 1 ($\Delta k \neq 0$) and Experiment 2 ($\Delta\omega_0 \neq 0$) Specified for Each Individual Participant

Variable	Participant 1	2	3	4	5	6	7	8	9
Characteristic									
M (kg)	69.2	65.8	70.2	77.2	78.0	73.3	69.2	78.0	81.2
leg_{left} (cm)	41.8	41.5	42.5	43.3	48.0	44.0	43.3	44.0	47.0
leg_{right} (cm)	41.8	41.5	43.0	43.2	48.0	43.8	43.3	44.0	47.0
$K_{pretest}$ (Nm·rad^{-1})	1.51	8.10	4.42	8.43	8.21	6.97	4.92	8.06	7.74
Experiment 1									
$f_{metronome}$ (Hz)	0.85	1.02	0.91	0.98	0.92	0.95	0.92	0.96	0.92
$\Delta k1$ (*10^{-2} rad·[Nm]$^{-1}$)	1.02	0.42	0.58	0.36	0.36	0.45	0.61	0.37	0.37
(%)	(16.9)	(9.5)	(12.2)	(9.1)	(9.7)	(10.4)	(12.4)	(9.5)	(9.8)
$\Delta k2$ (*10^{-2} rad·[Nm]$^{-1}$)	1.74	0.76	1.03	0.66	0.66	0.81	1.09	0.68	0.68
(%)	(28.9)	(17.2)	(21.7)	(16.6)	(17.7)	(18.7)	(22.0)	(17.2)	(17.4)
$\Delta k3$ (*10^{-2} rad·[Nm]$^{-1}$)	2.28	1.05	1.39	0.92	0.91	1.11	1.46	0.94	0.93
(%)	(37.9)	(23.7)	(29.4)	(23.0)	(24.3)	(25.6)	(29.7)	(23.5)	(24.6)
$\Delta k4$ (*10^{-2} rad·[Nm]$^{-1}$)	2.70	1.29	1.68	1.13	1.12	1.36	1.77	1.15	1.14
(%)	(44.7)	(29.1)	(35.5)	(28.3)	(29.8)	(31.3)	(35.9)	(29.2)	(30.1)
$\Delta k5$ (*10^{-2} rad·[Nm]$^{-1}$)	3.06	1.51	1.95	1.33	1.32	1.59	2.05	1.35	1.34
(%)	(50.7)	(34.0)	(41.1)	(33.3)	(35.1)	(36.6)	(41.6)	(34.2)	(35.4)
Experiment 2, k-level 1									
$\Delta\omega_0$ small (rad·s^{-1})	0.20	0.25	0.19	0.20	0.16	0.20	0.21	0.19	0.16
$\Delta\omega_0$ medium (rad·s^{-1})	0.42	0.52	0.41	0.43	0.35	0.43	0.44	0.40	0.35
$\Delta\omega_0$ large (rad·s^{-1})	0.97	1.16	0.94	1.00	0.81	0.99	1.00	0.93	0.81
Experiment 2, k-level 2									
$\Delta\omega_0$ small (rad·s^{-1})	0.24	0.29	0.24	0.25	0.21	0.25	0.25	0.24	0.21
$\Delta\omega_0$ medium (rad·s^{-1})	0.56	0.65	0.55	0.58	0.48	0.57	0.57	0.54	0.48
$\Delta\omega_0$ large (rad·s^{-1})	1.06	1.22	1.04	1.09	0.94	1.08	1.09	1.04	0.94

Note. M = body weight. leg = length of lower leg. K = estimated stiffness parameter. $f_{metronome}$ = prescribed movement frequency. $\Delta k = k_{right} - k_{left}$. $\Delta\omega_0 = \omega_{0\text{-right}} - \omega_{0\text{-left}}$. Relative differences in $k\{[(k_{right} - k_{left})/k_{right}] * 100\%\}$ are shown between parentheses. Note that Participant 6 was excluded from the analyses.

Pretest: Estimation of stiffness parameter K. To allow for estimating ω_0 and k for each individual participant (on the basis of Equations 7 and 8), we carried out a pretest to estimate parameter K, which reflects the rotational stiffness of the leg–lever system. To that end, the preferred movement frequency of the left leg–lever system was determined for 11 loading conditions in which a weight of 3 kg was attached at different distances from the knee joint (at 0.07–0.57 m, at intervals of 0.05 m). In addition, an unloaded condition was incorporated, which was measured twice[4] (i.e., 2×3 consecutive trials), that is, at the beginning and the end of the session. The order of the other experimental conditions (each examined in 3 consecutive trials) was randomized for each participant, which resulted in a total of 39 (13×3) trials. On the basis of the thus-obtained preferred movement frequencies (f), we estimated the stiffness parameter for the left leg–lever system (K_{left}), using nonlinear regression based on Equation 7 (with $\omega_0 = 2\pi \cdot f$). The stiffness parameter for the right leg–lever system (K_{right}) was assumed to equal K_{left}.

Experiment 1: Manipulation of Δk. In the first experiment, we chose load combinations that induced various values of Δk, whereas $\Delta\omega$ was approximately equal to 0. To that end, the right leg remained unloaded while mass perturbations were applied to the left leg at distance $R_{disc\text{-}left} = R_0$ (as estimated for each individual participant on the basis of Equation 6). By using five different masses (1–5 kg in 1-kg steps), we induced five different values for Δk while ω_0 remained similar for both legs (see Figure 3). In the control condition, both legs were unloaded ($\Delta k \approx 0$, and $\Delta\omega \approx 0$). For each participant, the estimated values of Δk resulting from those loading combinations are shown in Table 1.

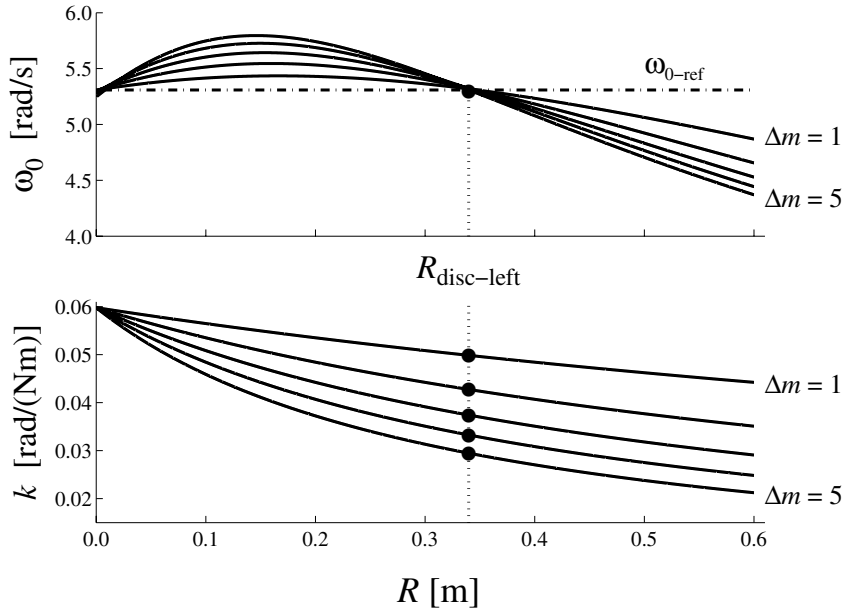

FIGURE 3. Mass perturbations applied in Experiment 1. The effects of added mass (Δm) and location of mass (R = distance between added mass and pivot point) on undamped eigenfrequency (ω_0; **upper panel**) and low-frequency control gain (k; **lower panel**), as calculated for Participant 1 on the basis of anthropometric estimates from Plagenhoef et al. (1983) in combination with the values presented in Table 1 (lower leg + foot segment: m = 4.27 kg, R_{cm} = 0.255 m, R_{gyr} = 0.309 m, and $I = m \cdot R_{gyr}^2$ = 0.4085 kg·m^2) and the set-up characteristics (lever: m = 0.56 kg, R_{cm} = 0.34 m, and I = 0.0876 kg·m^2; ankle support: m = 0.80 kg, R_{cm} = 0.34 m, and I = 0.0974 kg·m^2). In the experiment, we attached weights to the left leg at $R_{disc\text{-}left} = R_0$ so that the eigenfrequency (upper panel) of the loaded leg–lever system (left leg) equaled the eigenfrequency of the unloaded leg–lever system (right leg). Application of different masses (Δm = 1, 2, 3, 4, and 5 kg; masses associated with the outermost curves are indicated in the graphs) resulted in different low-frequency control gains (lower panel). R_{gyr} = radius of gyration of the (unperturbed) limb segment relative to the pivot point; R_{cm} = distance between the pivot point and the (unperturbed) segment's center of mass; $\omega_{0\text{-ref}} = \omega_0$ in the absence of mass perturbation.

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Two coordination modes were examined: in-phase and antiphase. The order of the six loading conditions (including the control condition) was randomized over the participants. For each loading condition, six trials were run: three consecutive trials for in-phase and three consecutive trials for antiphase coordination, with 5 participants starting with the in-phase mode and 4 starting with the antiphase mode. For each individual participant, the required movement frequency was based on ω_0 of the unloaded right leg–lever system (i.e., $\omega_{0\text{-ref}}$ in Figure 3), as estimated on the basis of Equation 7 (using the individual's anthropometric estimates and the estimated value of K). To obtain the required movement frequency (in Hz), we divided the obtained ω_0 by 2π. Thus, for each participant, a single pacing frequency was determined, which was prescribed by means of a metronome presenting two 200-Hz tones per cycle (i.e., one tone per half-cycle).

Experiment 2: Manipulation of $\Delta\omega$. For the second experiment, we chose load combinations that resulted in similar values of k for the two legs (estimated by using Equation 8; $\Delta k \approx 0$) but at the same time induced an imbalance in eigenfrequency ($\Delta\omega \neq 0$). Because the participants were instructed to oscillate both limbs at a common frequency, the preferred movement frequency was expected to fall in between the two uncoupled eigenfrequencies (Kugler & Turvey, 1987). To minimize muscular effort during the task, we did not prescribe movement frequency, and the participants were free to move at their own preferred frequency.

We included two different low-frequency control gain levels in the experimental conditions, corresponding to the values of k induced by adding loads of 1 and 2 kg, respectively, at 0.60 m from the knee (see Figure 4). For both k levels, the right leg was loaded with 5 kg at the position that induced the required value of k. The load for the left leg varied: For k-level 1, the left leg was loaded with 1, 2, or 3 kg; for k-level 2, it was loaded with 2, 3, or 4 kg. Figure 4 illustrates how the positions of those mass perturbations were determined. For each k level, the loading conditions resulted

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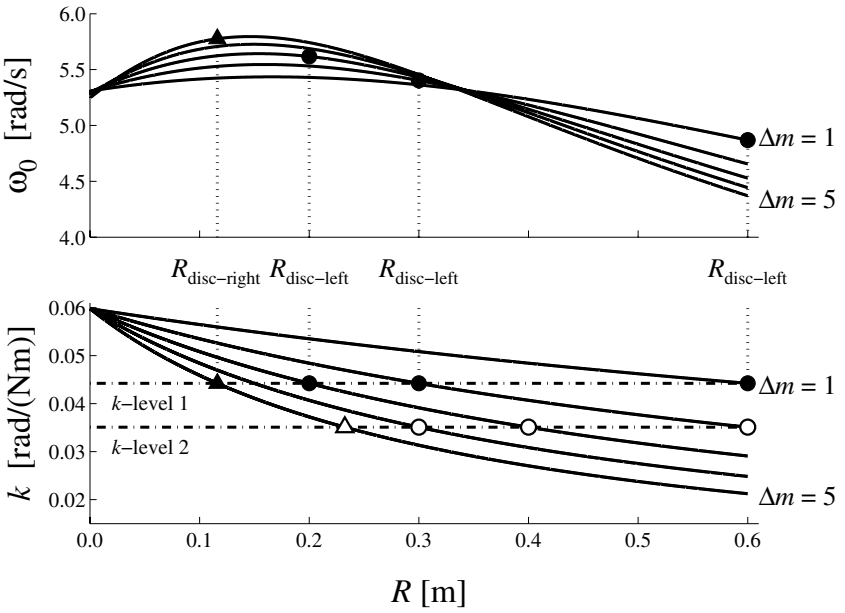

FIGURE 4. Mass perturbations applied in Experiment 2. The effects of mass (Δm = 1, 2, 3, 4, and 5 kg; masses associated with the outermost curves are indicated in the graphs) and location of mass (R = distance between added mass and pivot point) on eigenfrequency (ω_0; **upper panel**) and low-frequency control gain (k; **lower panel**) as calculated for Participant 1 (for characteristics of participant and set-up, see Figure 3). Two low-frequency control gain (k) levels were determined on the basis of the value of k as induced by a load of 1 kg (k-level 1) or 2 kg (k-level 2), respectively, positioned 0.60 m from the knee. In the lower panel, the position of mass addition to the right leg ($R_{\text{disc-right}}$) for k-level 1 = solid triangle, k-level 2 = open triangle. The position of mass addition to the left leg ($R_{\text{disc-left}}$) for k-level 1 = solid circles, k-level 2 = open circles. For k-level 1, the corresponding values of ω_0 are shown (upper panel). For that k-level, the right leg was loaded with 5 kg attached at 0.12 m from the knee, whereas the left leg was loaded with 1 kg attached at 0.6 m, 2 kg at 0.3 m, or 3 kg at 0.2 m from the knee, resulting in three different values of $\Delta\omega$. (The locations of the added weights were the same for each participant.) The ω_0 values for k-level 2 were derived in a similar manner.

in small, medium, and large eigenfrequency differences between the legs. The resulting values of $\Delta\omega$ for all conditions are shown in Table 1. In addition, we included two control conditions (one for each k level), which involved identical loading of the two legs (i.e., Δm = 5 kg; for both limbs, the additional mass was attached at $R_{\text{disc-right}}$ as determined for the corresponding k level; $\Delta\omega \approx 0$, and $\Delta k \approx 0$).

Experiment 2 was divided in two blocks of 24 trials. Each block (one for k-level 1 and one for k-level 2) consisted of the four $\Delta\omega$ conditions (including the associated control condition), the order of which was randomized for each participant. For each $\Delta\omega$ condition, 3 trials for in-phase and 3 for antiphase were run consecutively. Five participants started with k-level 1, and 4 began with k-level 2. Within those two groups, half of the participants started each condition in the in-phase mode, the other half with the antiphase mode.

Posttest: Estimation of stiffness parameter K. We carried out the posttest to examine whether the parameter estimation remained constant during the experiment. The procedure of the posttest was identical to that of the pretest (see earlier comments).

Data Analysis

We filtered the joint angle data by using a bidirectional second-order Butterworth filter with a cut-off frequency of 15 Hz. For each leg, movement amplitude—defined as $[(PE_i - PF_j) + (PE_{i+1} - PF_j)]/4$, where PE is peak extension and PF is peak flexion, with PF_j occurring between PE_i and PE_{i+1}—and movement frequency were determined per trial on the basis of the individual movement cycles, and subsequently were averaged over the three repeated trials. We calculated point estimates of relative phase (φ) by using the following equation:

$$\varphi = -\pi \cdot \frac{P_{\text{left}}(n) - P_{\text{right}}(m)}{P_{\text{right}}(m+1) - P_{\text{right}}(m)}, \tag{9}$$

where P is the index at which a peak (either flexion or extension) was observed, and $P_{\text{left}}(n)$ occurred in between $P_{\text{right}}(m)$ and $P_{\text{right}}(m + 1)$ (cf. Peper & Beek, 1998). By selecting extension peaks for both $P_{\text{left}}(1)$ and $P_{\text{right}}(1)$, one can unambiguously determine φ on the basis of the peak numbers (n, m). In that way, the phase of the left leg was determined relative to

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the phase of the right leg for each half-cycle (hence, multiplication by π rather than 2π). A negative value for φ indicated that the movements of the right leg were ahead in time compared with those of the left leg. Circular statistics were applied to average φ over the repeated trials (Mardia, 1972). Subsequently, for each participant, the mean deviation of φ from the required coordination pattern (i.e., $\Delta\varphi = \varphi - \varphi_{required}$, with $\varphi_{required} = 0$ for in-phase coordination and $\varphi_{required} = \pi$ for antiphase coordination) was determined for each experimental condition. The stability of coordination was indexed by the variability of the relative phasing between the lower legs, with low variability corresponding to a high degree of stability (cf. Schöner, Haken, & Kelso, 1986). To that end, we assessed the within-trial variability of φ (*Var*[φ]) by means of the transformed circular variance of φ (Mardia, 1972). That measure of variability is comparable to the ordinary standard deviation, with low values of the transformed circular variance indicating low variability.

The values of Δφ and *Var*(φ) as obtained for Experiment 1 were submitted to a 6 (Δ*k*) × 2 (coordination mode) analysis of variance (ANOVA) with repeated measures, whereas we examined the values obtained for Experiment 2 by using a 4 (Δω) × 2 (*k* level) × 2 (coordination mode) ANOVA with repeated measures. In addition, effect sizes (ε) were calculated for both experiments. Apart from significant effects ($p < .05$), tendencies toward significance ($p < .1$) are also presented.

Results

Estimation of Stiffness Parameter *K*

Explained variance of the individual regressions (r^2) was high, exceeding .9 in all cases except one (for the estimation of $K_{pretest}$ for Participant 1, $r^2 = .63$). For 7 of the 9 participants, the second estimation (based on the posttest, mean $K_{posttest} = 7.43$ Nm·rad^{-1}, *SD* = 1.53 Nm·rad^{-1}) exceeded the first (based on the pretest, mean $K_{pretest} = 6.48$ Nm·rad^{-1}, *SD* = 2.37 Nm·rad^{-1}). However, a paired *t* test revealed no significant difference between $K_{pretest}$ and $K_{posttest}$, $t(8) = 1.74$, $p = .119$. A representative example of the pre- and posttest eigenfrequency curves is shown in Figure 5.

Experiment 1: Manipulation of Δ*k*

In general, the performed movement frequency was close to the prescribed frequency, except for Participant 6. For him, the mean deviation from the prescribed frequency was 4.9% versus a mean deviation of –0.1% (*SD* = 0.2%) for the other participants. That finding implied that Participant 6 was not able to perform the task adequately (no frequency lock with the stimulus) and, therefore, we excluded the data obtained for that participant from further analysis (for both Experiments 1 and 2). The remaining 8 participants maintained an adequate mean within-trial movement amplitude; mean within-trial amplitude ranged from 11.2° to 16.2° (target amplitude = 14°, i.e., movement range = 28°; left leg mean amplitude = 14.4°, *SD* = 1.0°; right leg mean amplitude = 13.3°, *SD* = 0.9°).

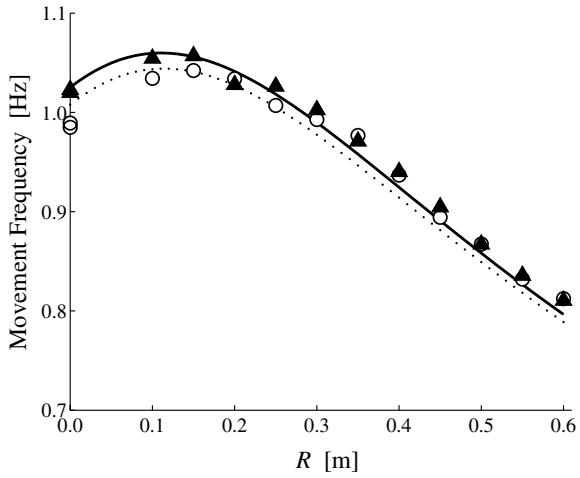

FIGURE 5. Preferred movement frequencies and corresponding regression curves as obtained for Participant 2. *R* represents the distance relative to the knee at which the additional mass (Δ*m* = 3 kg) was located. Circles and dashed line = pretest; $K_{pretest} = 8.10$ Nm·rad^{-1} ($r^2 = .94$). Triangles and solid line = posttest; $K_{posttest} = 8.90$ Nm·rad^{-1} ($r^2 = .98$). Note that movement frequency (*f*) is related to angular frequency (ω) by $f = \omega/2\pi$.

Statistical analysis revealed no significant effects of Δ*k* or coordination mode on Δφ. Mean Δφ was –0.069 rad (*SD* = 0.131 rad), indicating that the right leg was, on average, slightly ahead in time.

Although we also found no significant effects on *Var*(φ) (mean *Var*[φ] = 0.095, *SD* = 0.011), coordination mode tended to affect *Var*(φ) to some extent, $F(1, 7) = 3.63$, $p < .1$, $\varepsilon = .34$. Mean *Var*(φ) was 0.098 (*SD* = 0.035) for antiphase and 0.093 (*SD* = 0.031) for in-phase coordination.

Experiment 2: Manipulation of Δω

Movement frequency ranged from 0.93–1.05 Hz in the control conditions (equal loading of the two legs) and decreased gradually with Δω (frequency ranges for the Δω conditions small, medium, and large = 0.87–1.04, 0.87–1.00, and 0.80–0.95 Hz, respectively). Mean within-trial movement amplitude ranged from 11.2° to 16.7° over all conditions (*k*-level 1: mean amplitude = 13.9° [left] and 14.3° [right], *SD* = 0.9° [left] and 1.0° [right]; *k*-level 2: mean amplitude = 14.1° [left] and 14.3° [right], *SD* = 1.2° [left] and 1.0° [right]) for the 8 remaining participants (excluding Participant 6, see earlier comment).

The main effect of Δω, $F(3, 21) = 49.67$, $p < .01$, $\varepsilon = .88$, revealed that the effect on Δφ increased with Δω (see Figure 6A). Post hoc comparison (paired *t* tests, $p < .05$) revealed significant differences between all levels of Δω. Although the main effects of *k* level and coordination mode did not reach significance at the $p = .05$ level, those variables tended to affect Δφ: For *k* level, $F(1, 7) = 5.11$, $p < .1$, $\varepsilon = .42$; for coordination mode, $F(1, 7) = 4.47$, $p < .1$, $\varepsilon =$

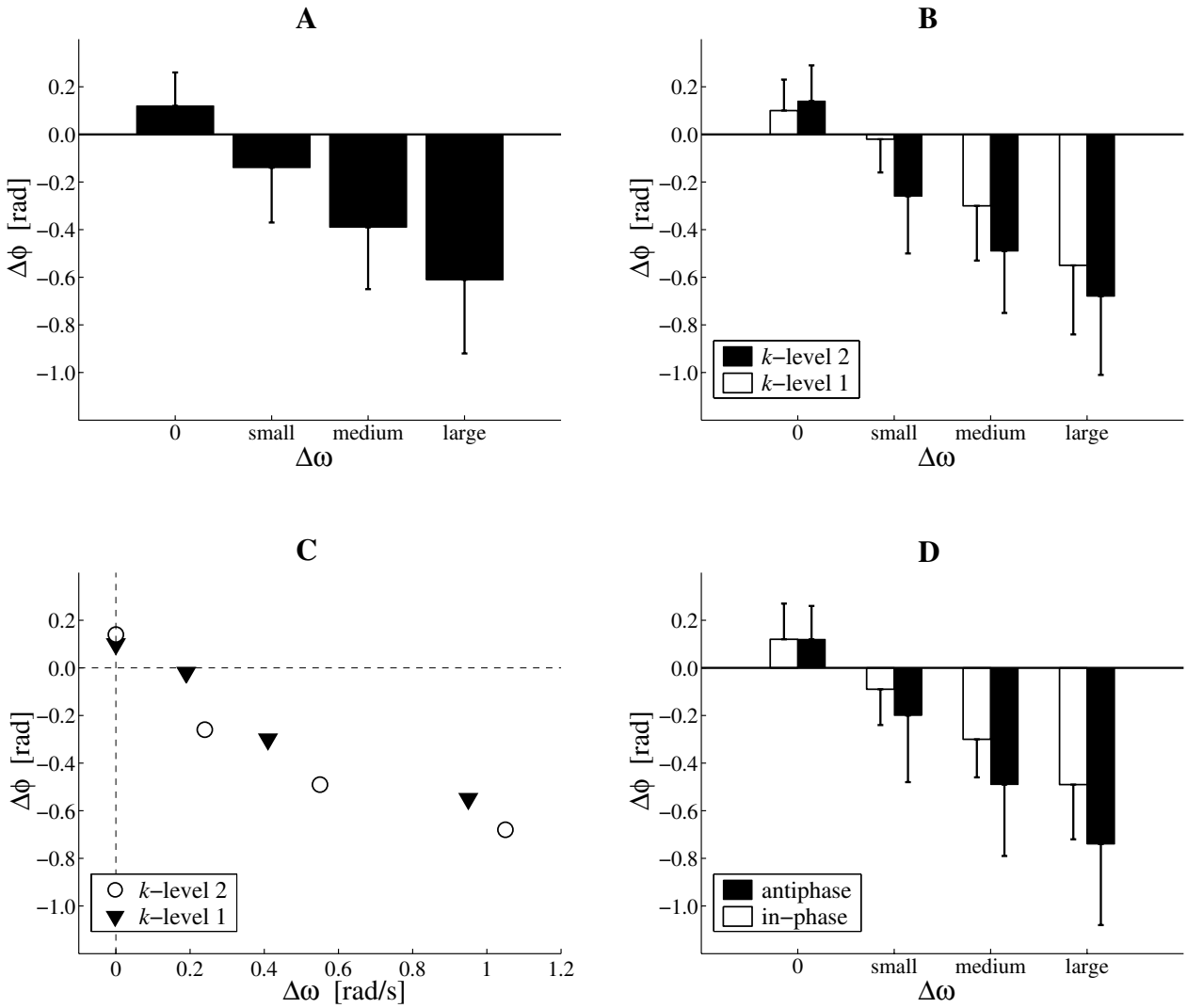

FIGURE 6. Mean Δφ (averaged over participants) as obtained for Experiment 2. **Panel A**. Effect of Δω. **Panel B.** Interaction between Δω and *k* level. **Panel C.** Mean Δφ (values averaged over coordination modes) plotted against the mean individual estimates of Δω (cf. Table 1), corresponding to the four Δω conditions, for the two *k* levels. **Panel D.** Interaction between Δω and coordination mode. Error bars represent 1 standard deviation.

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.39. Those nonsignificant trends reflected that the influence of *k*-level 2 on Δφ tended to be larger than that of *k*-level 1 (mean Δφ = –0.322 rad, *SD* = 0.393 rad, vs. –0.192 rad, *SD* = 0.326 rad, respectively) and that Δφ tended to be affected more strongly during antiphase coordination than during in-phase coordination (mean Δφ = –0.324 rad, *SD* = 0.289 rad, vs. –0.200 rad, *SD* = 0.420 rad, respectively).

The interaction between *k* level and Δω was also significant, $F(3, 21) = 5.84$, $p < .05$, $\varepsilon = .46$. Post hoc comparisons (paired *t* tests, $p < .05$) revealed that the effect of Δω on Δφ was more pronounced for *k*-level 2 than for *k*-level 1 (cf. Figure 6B). However, that result may have simply reflected the main effect of Δω, because *k*-level 2 involved larger values of Δω than did *k*-level 1 (see Table 1). That finding is illustrated in Figure 6C, where the plot of Δφ against the mean values of Δω (averaged over participants and coordination modes, for each Δω condition) that were applied in the two *k*-level conditions revealed that the effect on Δφ increased monotonically with increasing values of Δω.

The significant interaction between Δω and coordination mode, $F(3, 21) = 9.66$, $p < .001$, $\varepsilon = .58$, indicated that the effect of Δω was stronger during antiphase coordination than during in-phase coordination (see Figure 6D). Post hoc comparisons (paired *t* tests, $p < .05$) revealed that Δφ was not affected by coordination mode when $\Delta\omega \approx 0$, but that the effect on Δφ was larger for the antiphase mode than for the in-phase mode for all $\Delta\omega \neq 0$ conditions. The interaction between Δω and coordination mode was also reflected

by the significant interaction between *k* level and coordination mode, $F(3, 21) = 6.25$, $p < .05$, because *k*-level 2 (in-phase mean $\Delta\varphi = -0.235$ rad, $SD = 0.311$ rad; antiphase mean $\Delta\varphi = -0.409$ rad, $SD = 0.448$ rad) involved larger values of $\Delta\omega$ than did *k*-level 1 (in-phase mean $\Delta\varphi = -0.145$ rad, $SD = 0.263$ rad; antiphase mean $\Delta\varphi = -0.238$ rad, $SD = 0.378$ rad).

Var(φ) was more strongly affected during antiphase coordination than during in-phase coordination, $F(1, 7) = 7.98$, $p < .05$, $\varepsilon = .53$. Mean *Var*(φ) was 0.105 ($SD = 0.07$) for antiphase and 0.100 ($SD = 0.07$) for in-phase coordination.

Discussion

An often-advertised characteristic of the dynamical systems approach to human movement is its ability to capture coordination phenomena with concepts that are defined without reference to specific features of the movement system (e.g., see P. G. Amazeen, Amazeen, & Turvey, 1998; Beek, Peper, & Stegeman, 1995). In doing so, however, the dynamical equations remain opaque with respect to their real-life referents (e.g., see Carson & Riek, 1998; Rosenbaum, 1998). Therefore, linking model parameters to particular properties of the movement system may enhance the explanatory power of such abstract dynamical models (e.g., see Peper et al., 2004). The specific parameter of interest in this study was the detuning parameter used in the extended HKB model to describe symmetry-breaking phenomena in rhythmic interlimb coordination. On the basis of the theoretical results of Van Soest et al. (2004), we dissociated the effects of two covarying variables (i.e., $\Delta\omega$ and Δk) on the relative phasing between the lower legs (for both in-phase and antiphase coordination) by using mass perturbations. The deviation of the produced relative phase from the intended pattern ($\Delta\varphi$) and the variability of relative phase (*Var*[φ]) were used as indices of coordinative asymmetry and coordinative stability, respectively.

$\Delta\omega$ Induces Coordinative Asymmetries

In the first experiment, we applied mass perturbations that induced differences in the low-frequency control gains of the lower legs while we maintained similar undamped eigenfrequencies. We found that the imbalance in low-frequency control gain had no significant effect on either $\Delta\varphi$ or *Var*(φ). The second experiment involved manipulation of the difference in the undamped eigenfrequency while the low-frequency control gains were kept similar. The results showed that that manipulation influenced the relative phasing between the limbs: The phase shift increased with increasing values of $\Delta\omega$, and that effect was more pronounced for antiphase coordination than for in-phase coordination. In addition, the obtained difference in *Var*(φ) indicated that the antiphase mode was less stable than the in-phase mode.

The results of Experiment 1 indicated that the imposed asymmetry in low-frequency control gain did not induce an asymmetry in rhythmic interlimb coordination: The relative phasing between the limbs was not affected by an imbalance in the muscular torques that were required for adequate task performance. In combination with the clear phase shifts observed in Experiment 2 (i.e., in the absence of an imbalance in the low-frequency control gain), that finding suggests that the coordinative asymmetries induced by asymmetric mass perturbations applied to the coordinated limb segments are not caused by the resulting imbalance in low-frequency control gain. The fact that in the current experiments the required muscular torques were relatively low because the limbs were moved at approximately their undamped eigenfrequencies does not weaken that reading of the results, given the well-documented observation that the characteristic coordinative asymmetries are also observed at such movement frequencies (e.g., see Schmidt et al., 1993; Sternad et al., 1992). It remains to be established, however, whether interlimb coordination remains unaffected by an imbalance in low-frequency control gain when the required muscular effort is increased—for example, by oscillating the limbs at frequencies that differ considerably from their undamped eigenfrequencies.

In addition, the absence of an effect of Δk indicated that an asymmetry in another factor that covaries with eigenfrequency, namely, the moment of inertia (*I*), did not influence the phase relation between the limbs either. The moment of inertia of a limb segment increases monotonically with mass addition at increasing distances from the rotation point, with the increase in *I* being equal to $m_{disc} \cdot R^2_{disc}$ (cf. Equation 7). Thus, the difference between the limbs with respect to their moments of inertia covaried with the manipulations of Δk as applied in Experiment 1. That those manipulations did not affect the relative phasing between the limbs suggests that the associated differences in the moments of inertia also did not induce a coordinative asymmetry (which is in line with the results of Collins, Sternad, & Turvey, 1996).

Whereas the suggested influence of an imbalance in low-frequency control gain was not supported, the relative phases obtained for Experiment 2 clearly corroborated the common interpretation that a difference in eigenfrequency between the limbs induces an asymmetry in coordination (e.g., E. L. Amazeen et al., 1996; Jeka & Kelso, 1995; Kelso et al., 1990; Kelso & Jeka, 1992) and were in line with the predictions of the extended version of the HKB potential (Equation 1) when $\Delta\omega$ is incorporated as the detuning parameter (i.e., the phase shifts increased with $\Delta\omega$, and that effect was stronger for antiphase than for in-phase coordination). The HKB potential also leads to predictions with regard to the stability of coordination (e.g., see Kelso et al., 1990; Kelso & Jeka, 1992). In particular, according to the model, in-phase coordination is more stable than antiphase coordination and the induced shifts in relative phase are accompanied by decreased pattern stability. The first prediction was supported by the results of both experiments, although the difference between in-phase and antiphase coordination did not reach significance in Experiment 1.

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Contrary to the second prediction, the interaction between coordination mode and $\Delta\omega$ was not significant in Experiment 2, although the changes in $Var(\varphi)$ were in the expected direction. It is possible, however, that this tendency did not reach significance because of the relatively small variations of $\Delta\omega$ in Experiment 2 as compared with those in previous experiments (e.g., Sternad et al., 1996).

In sum, modeling the limb segments as forced linearly damped oscillators (in line with, e.g., Beek et al., 2002; Hatsopoulos, 1996; Jirsa & Haken, 1997; Sternad et al., 1998) allowed us to distinguish between the effects of imbalances with regard to two key parameters of such second-order systems, namely, their undamped eigenfrequencies and low-frequency control gains. The results indicated that the coordinative asymmetries induced by mass perturbations resulted from an imbalance in the eigenfrequencies of the coordinated limb segments (effector oscillators) rather than from an imbalance in low-frequency control gain.

How Can a Peripheral Mass Perturbation Influence the Coordination Process?

The present results indicate that in modeling the changes in the coordination dynamics that are induced by asymmetric mass perturbations, the detuning term in the extended HKB potential (Equation 1) is indeed related to the difference in eigenfrequency between the coordinated limbs.[5] Although the HKB potential adequately captures the resulting characteristics of the relative phase dynamics, a next question to be considered is how such a merely peripheral manipulation (mass addition) can inflict changes in the coordination between the limbs. On the basis of the two-level model construct (see introductory comments), one may explain part of the observed phase shifts on sheer mechanical grounds. It is well known that the phase relation between a forced (linear) oscillator and a sinusoidal forcing signal is affected by the difference between the eigenfrequency of the oscillator and the forcing frequency: The oscillation phase is delayed in time with respect to the forcing signal, and for a given forcing frequency the phase lag increases with decreasing eigenfrequencies of the forced oscillator (e.g., see Doebelin, 1998). Consequently, the relative phasing between two limbs with different eigenfrequencies may be expected to deviate from the relative phase as imposed by the corresponding control (forcing) signals. However, that peripheral effect cannot readily account for the observed changes in coordinative stability and the difference between in-phase and antiphase coordination with respect to the size of the induced phase shifts. Thus, whereas the manipulation was applied at the peripheral level (mass attached to limb segment), its effects appeared not to be limited to the effector level of our model but to extend to underlying control processes or, in model terms, either or both the neural oscillators and the interactions between them.

In that context, it is interesting to note that Baldiserra, Cavallari, Marini, and Tassone (1991) demonstrated that during rhythmic hand–foot coordination, loading the hand resulted in changes in the timing of the associated electromyographic (EMG) signals, which compensated for the induced phase lag (see also Mackey, Meichenbaum, Shemmell, Riek, & Carson, 2002). Perhaps the asymmetric changes in the timing of muscular activity that are required to compensate for the phase lags induced by asymmetric loading of two limbs (resulting in a difference in eigenfrequency) are related to the observed coordination phenomena. In addition, the suggestion that neural compensation may involve different mechanisms for in-phase and antiphase coordination (Baldissera, Borroni, & Cavallari, 2000) may be tentatively associated with the differential results obtained for those coordination modes.[6]

Another factor that might be related to the observed changes in coordination is the amount of additional effort (in terms of the magnitude of required muscular force) that is needed to move a limb at a frequency that differs from its eigenfrequency. In 1:1 frequency coordination between two limbs with dissimilar eigenfrequencies, at least one of the limbs is moved at a frequency that is not equal to its eigenfrequency. In principle, changes in the undamped eigenfrequency might be achieved by means of modulations of joint stiffness (i.e., through changes in the level of co-contraction of the agonist and antagonist muscles), which alter the dynamics of the limb segment. Thus, by means of additional muscular effort, the motor system may increase the segment's eigenfrequency so that it corresponds to the required movement frequency. As can be readily understood from Equation 5, however, the reach of that possible strategy is limited by the relation between the level of joint stiffness (K) that can actually be generated and the segment characteristics m, R_{cm}, and I ($= m \cdot R_{gyr}^2$). Moreover, it is hard to understand how a segment's eigenfrequency may be decreased below the value obtained for Equation 5 with $K = 0$, because that would require a reduction of the level of co-contraction below its absolute minimum.

Alternatively, the segment dynamics (including its eigenfrequency) may remain unaffected while the changes in movement frequency are induced by means of an adequate forcing pattern (i.e., adequately timed muscular activity). Forcing a limb segment to move at a frequency different from its own eigenfrequency requires more effort (in terms of the magnitude of forcing) than the required net muscular torque that is indicated by the low-frequency control gain of the limb segment. In particular, additional co-contractions may be expected to occur at the endpoints of the movement when the limb has to be decelerated and the movement direction is to be reversed (Bennett, Hollerbach, Xu, & Hunter, 1992). That those additional co-contractions are increased when a gravitational load is applied (Bennett et al.) may suggest that the characteristic asymmetries in the coordination between limbs with different eigenfrequencies are associated with an asymmetry in the muscular activity that is required to move them at a common frequency. From that perspective, the observation that the induced phase shifts grow with increasing movement frequencies (e.g.,

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P. G. Amazeen, Schmidt, & Turvey, 1995; Sternad et al., 1992) may be a reflection of an increasing asymmetry in the required muscular activity associated with the corresponding changes in the necessary levels of limb deceleration.

In view of the present experiments, it is useful to make a distinction between asymmetries in muscular activity associated with a difference in eigenfrequency (addressed previously) and those associated with a difference in low-frequency control gain. In Experiment 1, we examined the influence of the latter asymmetry while $\Delta\omega$ was approximately zero and the movements were paced at the estimated undamped eigenfrequency (ω_0) of the limb segments. As such, the considerations just addressed do not apply to those measurements, leaving the interpretation that a difference in k does not induce an asymmetry in relative phasing unaffected. Because a difference in low-frequency control gain implies simply that the gains of the forcing signals are unequal, the associated asymmetry in muscular activity is largely confined to a difference in the amplitude of that activity. This implication of a difference in low-frequency control gain can be readily contrasted with the implications of a difference in eigenfrequency delineated earlier, which involve an asymmetry between the limbs with regard to both amplitude and (in particular) the timing characteristics of the muscular activation patterns.

Whereas in the current experiments, we ensured that the required muscular torques were rather low, given the use of a small movement amplitude and movement frequencies at or close to the segments' eigenfrequencies, it is useful to discuss the consequences of substantial elevations of muscular torque as well. As was argued by Van Soest et al. (2004), elevations of muscle torque result in increased relative damping (β), which has two implications that are worth noting. First, for relatively high values of β, the distinction between the damped and the undamped eigenfrequency of a limb segment becomes more prominent, and, consequently, the eigenfrequency difference $\Delta\omega$ is to be defined in terms of the damped eigenfrequencies of the coordinated segments. Second, given the influence of β on the phase relation between a forcing (control) signal and a forced oscillator (e.g., see Doebelin, 1998), considerable increases in muscular torque may be expected to affect the phase relation between the coordinated limb movements. As argued earlier, however, this merely mechanical aspect of interlimb coordination does not provide an adequate account of typical coordination characteristics, such as the difference between coordination modes with regard to the induced phase shifts and the associated coordinative stability (cf. Schmidt & Turvey, 1995; Sternad et al., 1996). In addition, it cannot explain why low oscillation frequencies (i.e., lower than ω_0) result in reduced coordinative asymmetry (e.g., see Schmidt & Turvey, 1995; Sternad et al., 1992), given that moving at frequencies lower and higher than ω_0 both require increased muscular torque. Thus, to reiterate, it remains to be established how an imbalance in the (damped) eigenfrequencies inflicts asymmetries in the coordination process itself. In terms of the two-level model outlined in the introductory remarks, to do so would require determining how that characteristic of the effector oscillators affects the corresponding neural oscillators, their coupling, or both.

In summary, the results of the present experiments support the common interpretation that coordinative asymmetries induced by asymmetric mass perturbations are caused by a difference in the uncoupled eigenfrequencies. A next challenge resides in determining how such a merely peripheral property may affect the underlying coordination process. Identification of essential aspects in the control of the limb movements that are associated with the observed coordinative asymmetry (e.g., in terms of the timing or levels of required muscular activity, or both) may be helpful in linking the abstract coordination dynamics to underlying features of the movement system.

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NOTES

1. In the corresponding literature, no systematic distinction has been made between the damped and undamped eigenfrequencies of the component oscillators. In the studies that present estimations of the component eigenfrequencies, the influence of damping was not considered (cf., Kugler & Turvey, 1987).

2. In that context, it is useful to note that the effects of variations in the mass distribution of hand-held, physical pendulums (as applied in many studies; e.g., see Schmidt & Turvey, 1995) can be directly understood on the basis of Equation 2, with changes in the mass distribution of the hand-pendulum system corresponding to changes in m, R_{cm}, and R_{gyr} (with $\Delta m = 0$ and $R = 0$), thereby affecting both ω_0 and k (cf. Equations 5 and 4). The equivalent length (cf. Kugler & Turvey, 1987) of the resulting hand–pendulum system corresponds to R_0, as defined in Equation 6.

3. Note that in the study of Jeka and Kelso (1995), the location of mass addition to the lower arm + hand segment (close to the wrist joint) was also close to R_0 of that segment (cf. Plagenhoef et al., 1983). If that segment was oscillated as a hanging pendulum, then no substantial changes in the undamped eigenfrequency were to be expected. Because the oscillations were performed with the lower arm in an almost upright position, however, the applied mass perturbation probably still resulted in a decrease of the preferred movement frequency.

4. Because the potentiometer was located on the lever at the axis of rotation, the range at which the mass could be attached was physically limited. Given the diameter of the disc (0.09 m), the first part of the ω_0 curve could not be covered. To compensate for the limited resolution in this part of the ω_0 curve, we incorporated the unloaded condition twice.

5. Although our results indicated that the detuning term is related to $\Delta\omega$, it should be noted that it may not be exactly equal to that difference, because Sternad et al. (1995) and Collins et al. (1996) demonstrated that the coordinative asymmetries were related not only to the difference between the component eigenfrequencies but also to the ratio between them.

6. Baldissera et al. (2000) examined in-phase and antiphase coordination between ipsilateral hand and foot movements. They

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suggested that two different mechanisms were involved in adjusting the relative phasing between those different limb segments (with distinct dynamical properties). For in-phase coordination, a time delay was induced between the EMG activation of the hand and foot muscles (predominantly observed for male participants). For antiphase coordination, on the other hand, changes in the viscoelastic properties of one extremity were observed, which reduced the differences in the dynamical properties of the coordinated segments (observed for both male and female participants).

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8. Complete Mailing Address of Headquarters or General Business Office of Publisher *(Not printer)*: 1319 Eighteenth Street NW, Washington DC 20036-1802

9. Full Names and Complete Mailing Addresses of Publisher, Editor, and Managing Editor *(Do not leave blank)*

Publisher *(Name and complete mailing address)*: Helen Dwight Reid Educational Foundation, 1319 Eighteenth Street NW, Washington DC 20036-1802

Editor *(Name and complete mailing address)*: Board of Executive Editors, 1319 Eighteenth Street NW, Washington DC 20036-1802

Managing Editor *(Name and complete mailing address)*: Betty S. Adelman, 1319 Eighteenth Street NW, Washington DC 20036-1802

10. Owner *(Do not leave blank. If the publication is owned by a corporation, give the name and address of the corporation immediately followed by the names and addresses of all stockholders owning or holding 1 percent or more of the total amount of stock. If not owned by a corporation, give the names and addresses of the individual owners. If owned by a partnership or other unincorporated firm, give its name and address as well as those of each individual owner. If the publication is published by a nonprofit organization, give its name and address.)*

Full Name	Complete Mailing Address
Helen Dwight Reid Educational Foundation	1319 Eighteenth Street NW, Washington DC 20036-1802

11. Known Bondholders, Mortgagees, and Other Security Holders Owning or Holding 1 Percent or More of Total Amount of Bonds, Mortgages, or Other Securities. If none, check box → ☒ None

Full Name	Complete Mailing Address

12. Tax Status *(For completion by nonprofit organizations authorized to mail at nonprofit rates) (Check one)*
The purpose, function, and nonprofit status of this organization and the exempt status for federal income tax purposes:
☒ Has Not Changed During Preceding 12 Months
☐ Has Changed During Preceding 12 Months *(Publisher must submit explanation of change with this statement)*

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13. Publication Title: JOURNAL OF MOTOR BEHAVIOR			14. Issue Date for Circulation Data Below: September 2004	
15.		Extent and Nature of Circulation	Average No. Copies Each Issue During Preceding 12 Months	No. Copies of Single Issue Published Nearest to Filing Date
a.		Total Number of Copies *(Net press run)*	1,171	1,146
b. Paid and/or Requested Circulation	(1)	Paid/Requested Outside-County Mail Subscriptions Stated on Form 3541. *(Include advertiser's proof and exchange copies)*	516	477
	(2)	Paid In-County Subscriptions Stated on Form 3541 *(Include advertiser's proof and exchange copies)*	0	0
	(3)	Sales Through Dealers and Carriers, Street Vendors, Counter Sales, and Other Non-USPS Paid Distribution	233	224
	(4)	Other Classes Mailed Through the USPS	0	0
c.		Total Paid and/or Requested Circulation *[Sum of 15b. (1), (2),(3),and (4)]*	749	701
d. Free Distribution by Mail *(Samples, complimentary, and other free)*	(1)	Outside-County as Stated on Form 3541	41	55
	(2)	In-County as Stated on Form 3541	0	0
	(3)	Other Classes Mailed Through the USPS	0	0
e.		Free Distribution Outside the Mail *(Carriers or other means)*	37	37
f.		Total Free Distribution *(Sum of 15d. and 15e.)*	78	92
g.		Total Distribution *(Sum of 15c. and 15f)*	827	793
h.		Copies not Distributed	344	353
i.		Total *(Sum of 15g. and h.)*	1,171	1,146
j.		Percent Paid and/or Requested Circulation *(15c. divided by 15g. times 100)*	91	88

16. Publication of Statement of Ownership
☒ Publication required. Will be printed in the December 2004 issue of this publication. ☐ Publication not required.

17. Signature and Title of Editor, Publisher, Business Manager, or Owner: Douglas J. Knight — Executive Director — Date: September 29, 2004

I certify that all information furnished on this form is true and complete. I understand that anyone who furnishes false or misleading information on this form or who omits material or information requested on the form may be subject to criminal sanctions (including fines and imprisonment) and/or civil sanctions (including civil penalties).

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1. Complete and file one copy of this form with your postmaster annually on or before October 1. Keep a copy of the completed form for your records.
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3. Be sure to furnish all circulation information called for in item 15. Free circulation must be shown in items 15d, e, and f.
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5. If the publication had Periodicals authorization as a general or requester publication, this Statement of Ownership, Management, and Circulation must be published; it must be printed in any issue in October or, if the publication is not published during October, the first issue printed after October.
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